

# Combinatorial Signal Processing in an Insect

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**ABSTRACT:** Human language is combinatorial: phonemes are grouped into syllables, syllables are grouped into words, and so on. The capacity for combinatorial processing is present, in different degrees, in some mammals and birds. We used vibrational insects, *Enchenopa* treehoppers, to test the hypothesis of basic combinatorial processing against two competing hypotheses: beginning rule (where the early signal portions play a stronger role in acceptability) and no ordering rule (where the order of signal elements plays no role in signal acceptability). *Enchenopa* males use plant-borne vibrational signals that consist of a whine followed by pulses. We tested the above hypotheses with vibrational playback experiments in which we presented *Enchenopa* females with stimuli varying in signal element combinations. We monitored female responses to these playbacks with laser vibrometry. We found strong support for combinatorial processing in *Enchenopa*: in brief, females preferred natural-combination signals regardless of the beginning element and discriminated against reverse-order signals or individual elements. Finding support for the combinatorial rule hypothesis in insects suggests that this capability represents a common solution to the problems presented by complex communication.

**Keywords:** communication, mate choice, signal processing, phonology, syntax, vibrational signaling.

Many aspects of human communication and cognition are built on the basis of mental processing that gives rise to combinatorial and hierarchical structure. In language, this capacity groups sound phonemes into syllables, syllables into words, words into phrases, and so on—and it also creates structure in music, mathematics, and thinking (Pinker 1994; Hauser and Chomsky 2002; Pinker and Jackendoff 2005; Fitch 2010; Corballis 2011; Fitch and Martins 2014).

Combinatorial processing is hypothesized to have originated prior to modern humans and to be present, in different degrees, in other lineages (Fitch 2010). A key distinction is whether processing is only combinatorial or whether it is

also hierarchical and recursive. Basic combinatorial processing involves rules regarding the specific combinations (or orderings) of discrete signal elements that are acceptable to receivers. In human language, for instance, processing at this level combines sound phonemes to form words; for example, in English the sounds /k/, /æ/, and /t/ are combined to form the word “cat” (Bowling and Fitch 2015). Some authors refer to such processing as “phonology” (Fitch 2010:94) or “finite state grammar” (Zuberbühler 2019:2). Examples of this basic combinatorial processing can be found in some primates, bats, hyraxes, and birds (table 1). Combinatorial processing may go beyond the abovementioned basic level and generate hierarchical structuring by recursive embedding of combinations of signal elements (Pinker 1994; Hauser and Chomsky 2002; Pinker and Jackendoff 2005; Fitch 2010; Fitch and Martins 2014). In human language, processing at this level combines words to form phrases (e.g., “cats purr”) that can be further combined with other phrases and embedded in sentences and more complex structures (Bowling and Fitch 2015). Some authors refer to this type of processing as “syntax” (Fitch 2010:100) or “phrase structure grammar” (Zuberbühler 2019:2). Examples of this more complex combinatorial-hierarchical processing can be found in some whales and birds (table 1; Bergman et al. 2019; Suzuki et al. 2019).

Similarities in the capacity for combinatorial processing across different species may represent common descent or convergent solutions to the problems that animals face in complex environments and complex communication systems (Fitch 2010). Consequently, understanding the evolution of combinatorial processing in animals, as well as the course it followed in our lineage, requires exploring the diversity and taxonomic distribution of combinatorial processing capabilities among animals.

Here we report basic combinatorial processing in the communication system of an insect, a member of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Enchenopa* treehoppers are phloem-feeding insects that communicate with plant-borne vibrational signals (Cocroft and Rodríguez 2005; Cocroft et al. 2008). Males produce advertisement signals consisting of

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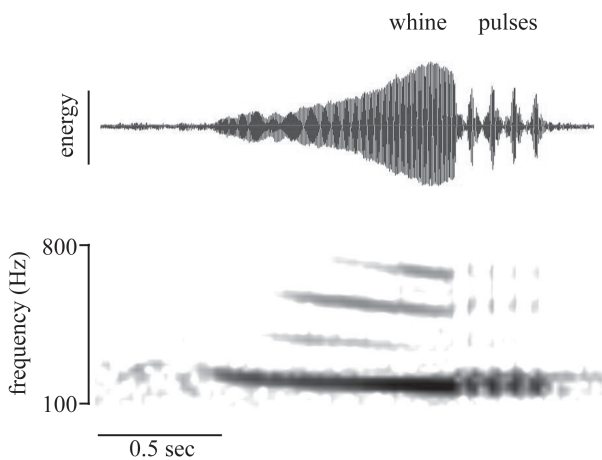
**Table 1:** Examples of basic and hierarchical combinatorial processing in animals

Species	Method of testing	Reference
Basic combinatorial processing:		
Birds:		
Black-capped chickadee ( <i>Parus atricapillus</i> )	Structure of naturally occurring calls	Hailman et al. 1987
Swamp sparrow ( <i>Melospiza georgiana</i> )	Ability to learn test sequences	Marler and Peters 1988
Yellow-naped amazons ( <i>Amazona auropalliata</i> )	Structure of naturally occurring calls	Dahlin and Wright 2009
Java sparrows ( <i>Lonchura oryzivora</i> )	Structure of spontaneously occurring calls in tutored and nontutored males	Soma and Mori 2015
Chestnut-crowned babbler ( <i>Pomatostomus ruficeps</i> )	Habituation	Engesser et al. 2019
Great tit ( <i>Parus major</i> )	Innate response to playbacks	Dutour et al. 2019
Coal tit ( <i>Periparus ater</i> )	Innate response to playbacks	Dutour et al. 2019
Common chaffinch ( <i>Fringilla coelebs</i> )	Innate response to playbacks	Dutour et al. 2019
Primates:		
Wedge-capped capuchins ( <i>Cebus olivaceus</i> )	Structure of naturally occurring calls	Robinson 1984
Cotton-top tamarins ( <i>Saguinus Oedipus</i> )	Habituation	Fitch and Hauser 2004
Chimpanzee ( <i>Pan troglodytes</i> )	Structure of naturally occurring calls	Crockford and Boesch 2005
Putty-nosed monkey ( <i>Cercopithecus nictitans</i> )	Innate response to playbacks	Arnold and Zuberbühler 2008
Campbell's monkeys ( <i>Cercopithecus campbelli campbelli</i> )	Structure of naturally occurring calls and innate response to playbacks	Ouattara et al. 2009
Red-capped mangabeys ( <i>Cercocebus torquatus</i> )	Structure of naturally occurring calls in captivity	Bouchet et al. 2010
Titi monkey ( <i>Callicebus nigrifrons</i> )	Structure of naturally occurring calls	Cäsar et al. 2013
Western gorilla ( <i>Gorilla gorilla</i> )	Structure of naturally occurring calls	Hedwig et al. 2015
Mountain gorilla ( <i>Gorilla beringei beringei</i> )	Structure of naturally occurring calls	Hedwig et al. 2015
Geladas ( <i>Theropithecus gelada</i> )	Innate response to playbacks	Gustison and Bergman 2016
Bonobos ( <i>Pan paniscus</i> )	Structure of naturally occurring calls	Schamberg et al. 2016
Rhesus macaques ( <i>Macaca Mulatta</i> )	Ability to learn test sequences	Heimbauer et al. 2018
Other mammals:		
Mustached bat ( <i>Pteronotus parnellii parnellii</i> )	Structure of naturally occurring calls	Kanwal et al. 1994
Rock hyrax ( <i>Procavia capensis</i> )	Innate response to playbacks	Kershenbaum et al. 2012
Hierarchical combinatorial processing:		
Birds:		
Song sparrow ( <i>Melospiza melodia</i> )	Ability to learn test sequences	Marler and Peters 1988
European starlings ( <i>Sturnus vulgaris</i> )	Habituation	Gentner et al. 2006
Yellow-naped Amazons ( <i>Amazona auropalliata</i> )	Structure of naturally occurring calls	Dahlin and Wright 2009
Cassin's Vireos ( <i>Vireo cassinii</i> )	Innate response to playbacks	Hedley et al. 2017
Other mammals:		
Humpback whales ( <i>Megaptera novaeangliae</i> )	Structure of naturally occurring calls	Allen et al. 2019

two elements: a whine (W) followed by a series of pulses (P; Cocroft et al. 2010; fig. 1). This WP signal structure is highly conserved in the *E. binotata* complex, while other signal features (especially dominant frequency) are strongly species specific and covary with divergent female preferences (Rodríguez et al. 2006; Cocroft et al. 2008, 2010). This conservation of basic signal structure against the background of strong divergence in other traits suggests either strong stabilizing selection on signal structure or strong signal-production constraints. While PW variants are observed only rarely in the *E. binotata* complex (R.B. Cocroft, personal communication), reversals in signal structure

are common across species in treehoppers and other vibrational insects (Cocroft 2003; Percy et al. 2006, 2008). This observation argues against production constraints, and we therefore focus here on testing for a female combinatorial processing rule for signal structure in *Enchenopa* treehoppers.

We tested the combinatorial rule hypothesis in terms of the *Enchenopa* communication system and the two-element (WP) structure of male advertisement signals (predictions i–iii in table 2). We tested this hypothesis against two competing alternatives. First, signal processing might not be truly combinatorial; instead, earlier elements



**Figure 1:** The two-element male advertisement signal of *Enchenopa* treehoppers, shown as an oscillogram (top) and spectrogram (bottom).

may simply have stronger effects on signal acceptability than later signal elements. There is evidence in support of this hypothesis from studies in some insects and frogs, which have referred to the “temporal-order effect” hypothesis (Gerhardt et al. 2007; Reichert et al. 2017). We use the term “beginning rule” to emphasize that this hypothesis focuses on the strength of the effect of the beginning of signals rather than on the combination of elements per se (prediction iv in table 2). The second competing hypothesis is the null or “no ordering rule” hypothesis, whereby many possible arrangements of signal elements are acceptable (prediction v in table 2). There is evidence in support of this hypothesis

from studies in some frog species (Wilczynski et al. 1999; Oliva et al. 2018).

We also contrasted the response to the natural-combination stimulus (WP) against the single element stimuli (W and P). These tests do not directly address the logic of the hypotheses, but inform us of the relative importance of the presence of each signal element per se.

We tested the predictions described above (table 2) with a vibrational playback experiment in which we presented *Enchenopa* females with synthetic stimuli varying in signal element composition to assess their acceptability. The combinatorial processing literature includes a very broad range of methods, from analysis of the structure of naturally occurring signals to experiments requiring sophisticated learning abilities in the animals to test the hypotheses (table 1). Our experiment tests for differences in female responsiveness to stimuli varying in signal element combinations. It makes no assumptions about whether those differences are innate or acquired (although the former seems likely). The tests involve potential effects from preceding signal elements on subsequent signal elements (combinatorial rule and beginning rule hypotheses). We therefore presented each female with only one stimulus. Our experiment thus assessed variation in the responses of females across stimuli to test for population-level rules regarding signal element combinations.

Methods

We worked with one of the two *Enchenopa binotata* species that live on *Viburnum lentago* (Adoxaceae) bushes and trees in Wisconsin. Most of the species in the complex have

Table 2: Hypotheses that analyze processing of signal element combinations in <i>Enchenopa</i> treehoppers as well as their predictions		
Hypothesis	Prediction	Summary
Combinatorial rule	Prediction i: females should prefer the natural-combination stimulus over a reverse-order stimulus	WP > PW
	Prediction ii: females should make no distinction between the natural-combination stimulus and a stimulus beginning with the wrong element but containing the natural combination stimulus	WP = PWP
	Prediction iii: females should prefer a stimulus beginning with the wrong element but containing the natural combination stimulus over a reverse-order stimulus	PWP > PW
Beginning rule	Prediction iv: females should prefer stimuli with the natural-beginning element over stimuli beginning with the wrong element	WP > PW WP > PWP W > PW W > PWP
No ordering rule	Prediction v: females should make no distinction between stimuli with different signal element combinations	WP = PW = PWP

Note: We did not contrast the response to whine (W) and pulse (P) stimuli because this comparison might depend not only on the beginning of the P stimulus but also on it being insufficient on its own.

not yet been formally described (Hamilton and Cocroft 2009), but they can be distinguished by their host plant, nymph coloration, and the dominant frequency of adult male signals (Wood 1980, 1993; Rodríguez et al. 2004; Cocroft et al. 2008, 2010). We used the species that has male signals with a dominant frequency of 185 Hz.

We conducted the study over the summers of 2016 and 2017. In 2016, we collected the treehoppers in June as late instar nymphs at the University of Wisconsin–Milwaukee's (UWM's) Downer Woods and then reared them to maturity on potted *V. lentago* plants in the UWM greenhouse. In 2017, we used nymphs reared from eggs that we hatched in the greenhouse ahead of the summer season.

We separated adult females from males 1–3 days after their final molt. Separation was essential to prevent the females from mating, thus keeping them sexually receptive and responsive to playbacks. We began our trials when the females reached sexual maturity, 4 weeks after the adult molt.

We created vibrational playback stimuli on an iMac computer using Matlab version 7.5.0.338 (Mathworks, Natick, MA; <http://www.mathworks.com>). The playback stimuli varied in the combination of signal elements presented to females as follows: stimuli had either the natural whine-pulse (WP) signal element combination, the reverse pulse-whine (PW) element combination, a pulse-whine-pulse (PWP) element combination, a single whine (W) element, or a single pulse (P) element. We set all other stimulus features to the population mean (185 Hz dominant frequency, 950 ms whine length, 3 pulses, 38 ms pulse length, and 21 Hz pulse rate; R. L. Rodríguez unpublished data), except that we used only one signal per stimulus rather than the typical signal bout structure (Cocroft et al. 2010) to avoid possible confounding effects of preceding stimuli on subsequent stimuli (a possibility under the combinatorial and beginning rule hypotheses).

We presented each female with a single, randomly assigned playback stimulus (i.e., we tested each female only once). Thus, responses to each stimulus by each female are fully independent of each other. Furthermore, this was necessary in our study because of the potential for confounding effect of preceding stimuli on subsequent stimuli (see the rationale described above).

To present females with a playback stimulus, we placed each female singly on a small potted *V. lentago* plant and allowed her to roam and settle (for a minimum of 30 s and a maximum of 10 min) before presenting her with a single, randomly selected stimulus. *Enchenopa* females that find a male's signal attractive respond with their own single-element signals, establishing a duet that lasts until mating begins (Rodríguez and Cocroft 2006; Cocroft et al. 2008; Rodríguez et al. 2012). Our assay of stimulus acceptability took advantage of this aspect of the *Enchenopa* communication system: we noted whether a female produced a du-

etting signal in response to the stimulus. If the female did not respond to the stimulus, we presented her with the playback of a recording of a male signal to confirm that she was sexually receptive and that she did not respond to the experimental stimulus because it was unattractive to her. If she did not respond to the playback of the recorded male, we retested her 1–3 days later. We tested  $n = 40$  females for each of the five stimuli ( $n = 20$  females per stimulus per year).

We imparted the playback stimuli onto the test plant with a piezo-electric controller and actuator (Thorlabs, Newton, NJ) attached to its stem with wax. We delivered all stimuli at a peak amplitude of 0.15 mm/s.

We recorded the stimuli and female responses with a laser vibrometer (Polytec PLV-100; Polytec, Auburn, MA). We sent the output of the laser vibrometer through a bandpass filter (40–4000 Hz; Krohn-Hite 3202; Krohn-Hite, Brockton, MA) and digitized it on an iMac with a sampling rate of 44.1 kHz using the program Audacity (ver. 2.1.2; [www.audacityteam.org](http://www.audacityteam.org)). After testing, we returned females to the laboratory colony or to the field (Downer Woods).

### Statistical Analysis

We conducted the statistical analysis in two steps. We first tested for variation in the likelihood of female response to the different stimuli. The model had female response (0 for no response, 1 for response) as the dependent variable. The error structure was a binomial distribution. The explanatory variables were stimulus (i.e., signal element combination), year, and their interaction. Because of complete separation in the data (0% response for one stimulus; see below), the maximum likelihood estimates of the regression coefficients could not be estimated, as they do not exist (Albert and Anderson 1984). We therefore used a Bayesian generalized linear model with a Cauchy prior (Gelman et al. 2008). We fit the model in R using the function `bayesglm` of the `lme4` package (ver. 1.10-1; Gelman and Su 2018). We checked model stability by excluding data points one at a time from the data set and found that all the coefficient estimates were stable. We derived variance inflation factors (Field 2009) with the `vif` function of the `car` package (ver. 3.0-3; Fox and Weisberg 2011). We found no collinearity between fixed effects.

The second step of our analysis was to test each of the predictions specifically (table 2). To this end, we used Tuckey post hoc tests to compare the response to each of the relevant stimulus pairs. We obtained these comparisons from a model with only the main terms (stimulus and year), as their interaction was not significant. Data for these analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.r4xgxd28v>; Speck et al. 2020).

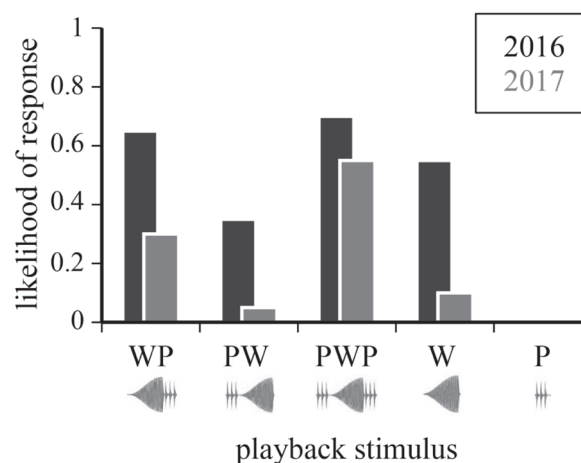


## Results

*Enchenopa* females varied in their likelihood to respond to the playback stimuli according to signal element combinations (significant stimulus term in table 3; fig. 2). The term for year was also significant, with females tested in 2016 being overall more responsive than those tested in 2017 (table 3; fig. 2). However, the stimulus  $\times$  year interaction was not significant (table 3), indicating that the patterns of response were similar across years (fig. 2). On the basis of the above overall effect of stimulus signal element combination on female responses, we used post hoc tests to pinpoint the comparisons specified by the hypotheses' predictions (table 2).

In support of the combinatorial rule hypothesis, *Enchenopa* females were significantly more likely to respond to the natural-combination stimulus (WP) than to the reverse-order stimulus (PW; table 4; fig. 2; supporting prediction i). Females were also about as likely to respond to the natural-combination stimulus (WP) as to the stimulus containing the natural combination but beginning with the wrong element (PWP); the difference in response was small and nonsignificant (table 4; fig. 2; supporting prediction ii). Females were also significantly more likely to respond to the natural-combination beginning with the wrong element (PWP) than to the reverse-order stimulus (PW; table 4; fig. 2; supporting prediction iii).

The comparison between the natural-combination stimulus (WP) to the reverse-order stimulus (PW) would also support the beginning rule hypothesis (table 4; fig. 2; prediction iv). However, in opposition to prediction iv, we found the following results: *Enchenopa* females were not significantly more likely to respond to the natural-combination stimulus (WP) than to the stimulus containing the natural combination but beginning with the wrong element (PWP; table 4; fig. 2), they were not more likely to respond to the single whine element stimulus (W) than to the reverse-order stimulus (PW; table 4; fig. 2), and they were significantly more likely to respond to the natural-combination stimulus



**Figure 2:** Tests for combinatorial signal processing in *Enchenopa* treehoppers. We show the likelihood of response to the playback stimuli: the natural-combination stimulus (WP), the reverse-order stimulus (PW), the stimulus beginning with the wrong element but containing the natural combination (PWP), the single whine element stimulus (W), and the single pulse element stimulus (P). Black bars = 2016 data; gray bars = 2017 data.

beginning with the wrong element (PWP) than to the single whine element stimulus (W; table 4; fig. 2).

Additionally, the overall significant effect of the stimulus term (table 3) and the predominance of significant comparisons supporting the combinatorial rules hypothesis (table 4; fig. 2) reject prediction v of the null no ordering rules hypothesis. Finally, *Enchenopa* females tended to be more likely to respond to the natural-combination stimulus (WP) than to either of the single-element stimuli (W or P), but only significantly so against the P stimulus (table 4; fig. 2).

## Discussion

We tested for basic combinatorial signal processing in *Enchenopa* treehoppers with playback experiments varying signal element structure. We found that *Enchenopa* females were more likely to respond to the natural-combination stimulus (WP) than to the reverse-combination (PW) stimulus. Interestingly, they were not more likely to respond to the natural-combination stimulus (WP) than to the natural-combination stimulus with the wrong element tacked in front (PWP), but they were more likely to respond to the latter than to the reverse-combination (PW) stimulus. They also were more likely to respond to the natural-combination stimulus with the wrong beginning element (PWP) than to the single whine element (W) stimulus, but they were not

**Table 3:** Analysis of variation in the likelihood of *Enchenopa* female response to vibrational playback stimuli varying in element composition

Term	df	<i>z</i>	<i>P</i>
Stimulus	4	55.74*	<.001*
Year	1	19.85*	.0013*
Stimulus $\times$ year	4	1.22	.87

Note: We used a Bayesian generalized linear model with a binomial error distribution to test the effect of the playback treatments, year of testing, and the playback  $\times$  year interaction (model explanation in text). The main terms remain nearly identical after removing the nonsignificant interaction (stimulus:  $z = 54.51$ ,  $P < .0001$ ; year:  $z = 18.63$ ,  $P < .0001$ ).

\* Significant term.

**Table 4:** Comparison of the likelihood of *Enchenopa* female response according to stimulus pairings that address the predictions of the hypotheses

Stimulus comparison <sup>a</sup>	<i>z</i>	<i>P</i>	Predictions supported	Predictions rejected
WP–PW	2.71*	.0497*	i, iv	v
WP–PWP	–1.44	.59	ii	iv
PWP–PW	3.92*	<.0001*	iii	iv, v
W–PW	1.34	.65		iv
W–PWP	–2.82*	.037*		iv, v
WP–W	1.46	.58		
WP–P	4.22*	<.0001*		v
W–P	3.30*	.0078*		v

Note: We show the results of the post-hoc tests from the Bayesian generalized linear model that included only the main terms for stimulus and year (see text and table 3). Abbreviations are as in table 2.

<sup>a</sup> There are two additional comparisons that we do not emphasize because they do not address any specific prediction; reported here for completeness: PW–P: *z* = 2.34, *P* = .13; PWP–P: *z* = 5.03, *P* < .001.

\* Significant term.

more likely to respond to the single whine element (W) stimulus than to the reverse-order stimulus (PW). These results thus strongly support the combinatorial rule hypothesis and strongly oppose the beginning rule and no ordering rule hypotheses (table 2).

A potential confounding factor in these tests is that some stimuli varied not only in element combination but also in length, potentially influencing female responses because of the overall strength of the stimulation provided (e.g., the WP stimulus may have stimulated females more strongly than the single-element stimuli, and the PWP stimulus may have stimulated females more strongly than the WP stimulus or the W stimulus). We consider, however, that this is not an important confounding factor in our results. First, *Enchenopa* mate preferences for signal length favor intermediate values (with the preferred length varying across species), rather than longer values (Rodríguez et al. 2004, 2006). Thus, a simple response to stronger stimulation in longer stimuli is unlikely to have an influence in our data. Furthermore, in a crucial test (WP vs. PW), the competing stimuli had the same length but varied in acceptability: this pinpoints element combination as the key factor. Additionally, some nonsignificant comparisons involved stimuli of different lengths (WP vs. PWP, W vs. PW, and WP vs. W), with the pattern in one of those being of greater response to the shorter stimulus (W vs. PW; table 4; fig. 2). We therefore conclude that any effect of stimulus length was at best secondary to the effect of signal element combinations.

Variation in female responsiveness over the 2 years of testing may be due to females in the second year being slightly younger than those in the first year (or to additional variables arising from working with field-collected vs. greenhouse-reared treehoppers; e.g., early development effects). Nevertheless, the patterns of signal acceptability that

we detect were robust to those differences. We therefore interpret our results in terms of the effect of signal element composition.

Thus, our results support the combinatorial rule hypothesis and reject the competing beginning rule and no ordering rule hypotheses: signal processing in *Enchenopa* includes rules about the combination of the two elements of male signals. If these rules are conserved across the *E. binotata* complex, they may explain the highly conserved structure of male advertisement signals in spite of remarkable signal preference codivergence in continuous signal features (especially dominant signal frequency; Rodríguez et al. 2006; Cocroft et al. 2008, 2010). However, structure reversal across different species is widespread in animals that communicate with substrate-borne vibrational signals (e.g., Cocroft 2003; Percy et al. 2006, 2008). This observation suggests that the rules that govern the combinations of signal elements that are acceptable to receivers also diverge frequently.

We might have initially expected combinatorial rules to be categorical, that is, to render signal element combinations either acceptable or completely unacceptable. However, although stimuli with the wrong combinations considerably lowered female responsiveness, only a few stimuli were consistently rejected by a large majority of females (fig. 2). It will therefore be interesting to explore the nature of the relationship between combinatorial rules and preferences for continuous signal traits (such as signal frequency) and the different forms that this relationship may take across different species.

We note that our experiment may not have probed the limit of *Enchenopa* combinatorial capabilities; it remains to be tested whether they may have more sophisticated hierarchical capabilities. Some insects and spiders have far more elaborate multielement signals than *Enchenopa*. Some jumping spiders, for instance, have multimodal signals that

rival the most elaborate displays of vertebrates in complexity (e.g., Girard et al. 2011; Elias et al. 2012). Higher-level combinatorial processing than we have documented here may be involved in such cases.

Shared combinatorial processing capabilities across vertebrates and invertebrates most likely represents convergence, rather than common descent, as the last common ancestor of these groups likely had a simple neural system (Feinberg and Mallatt 2016). Further studies will be required to see how widespread this capability is in invertebrates. We conclude, however, with the suggestion that combinatorial processing may represent a common solution to the problems presented by complex communication in a complex world.

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### Statement of Authorship

B.S. participated in the design of the study, coordinated and carried out field and lab work, participated in data analysis and in statistical analysis, and drafted the manuscript; S.S. carried out field and lab work and participated in data analysis; S.B. carried out field and lab work and participated in data analysis; S.J. carried out field and lab work and participated in data analysis; C.C. carried out field and laboratory work and participated in data analysis; and C.D. conducted the statistical analysis and helped write the manuscript. R.L.R. conceived, designed, and coordinated the study; carried out statistical analysis; and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

### Data and Code Availability

Data for these analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.r4xgxd28v>; Speck et al. 2020).

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